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A Working Framework for Quantifying Carbon Sequestration in Disturbed Land Mosaics

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ABSTRACT / We propose a working framework for future studies of net carbon exchange (NCE) in disturbed landscapes at broad spatial scales based on the central idea that landscape-level NCE is determined by the land mosaic, including its age structure. Within this framework, we argue that the area-of-edge-influence (AEI), which is prevalent in many disturbed, fragmented landscapes, should constitute a distinct ecosystem type since numerous studies have indicated unique ecological properties within these areas. We present and justify four working hypotheses currently being tested in northern Wisconsin, based on this framework: (1) the area of an ecosystem that is influenced by structural edges (e.g., AEI) has NCE that is significantly different from the ecosystem interior; (2) age structure and composition of an ecosystem play critical roles in determining the ecosystem's contribution to the cumulative net ecosystem production (*NEP*) of the landscape mosaic; (3) the relative importance of different structural and biophysical controls of carbon exchange is ecosystem dependent; and (4) the frequency and intensity of disturbances in time and space control the cumulative NCE of the land mosaic through alteration of ecosystems that vary in age, structure, physical environment, and interactions. In addition, we describe five different research approaches to quantify NCE at broad scales, including biometric estimations, ecophysiological methods, micrometeorological methods, applications of remote sensing and GIS, and ecosystem models.

Much recent scientific effort has been expended in measuring long-term exchanges of CO_2 between vegetation and the atmosphere in an attempt to determine the role terrestrial ecosystems play in the global carbon budget. Understanding the functioning of terrestrial ecosystems as net sources or sinks of carbon is central to understanding the terrestrial carbon cycle at landscape and regional scales. Currently, approximately half of the carbon released into the atmosphere from burning of fossil fuels is unaccounted for in global carbon models (Amthor 1995), suggesting the carbon storage capacity of either oceans or terrestrial systems is larger than previously thought. Terrestrial ecosystems have been hypothesized to be a sink for this increased concentration of atmospheric carbon (Tans and others 1990, Denning and others 1995, Walker and Steffen 1997, Fan and others 1998) and thus to account for the missing carbon within the global carbon budget (Turner and others 1995). However, much uncertainty exists in determining the location of the missing carbon due to natural variability in carbon pools and fluxes among the different terrestrial ecosystems (Sarmiento and Wofsy 1999). Factors that influence processes controlling net carbon uptake include physiological differences in forest functional groups and developmental stages, time since disturbance, management practices, climate, and nutrition status. Field studies on whole ecosystem CO_2 exchange, coupled with small-scale studies of physiological and biophysical processes, and evaluation of ecosystem process models have been intensified to bridge the gap between organismal, stand-level, and regional understanding of processes.

KEY WORDS: Carbon flux; Land mosaics; Management and disturbance; Eddy-covariance method; Ecosystem modeling; Soil respiration

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The recent sequestering of carbon in temperate regions is thought to be linked with forest regrowth in disturbed landscapes (Turner and others 1995, Potter and Klooster 1999). It has been estimated that 55% of US forest cover in the continental United States exists in stands or plantations in various stages of growth or regrowth, whereas the remaining 45% has been converted to other land uses (Turner and others 1993, Nemani and Running 1995). This suggests that flux measurements obtained solely within mature stands may not be representative of the overall landscape mosaic and therefore limit the applicability of these results at broader spatial scales. Yet, most prior and current efforts to quantify ecosystem-level carbon flux have focused on little-disturbed mature or late-successional ecosystems. One notable exception is the CarboEurope Cluster program of the European Union, under which projects have been developed to address the questions of disturbance and scale as related to carbon flux (*http://www.bgc-jena.mpg.de/public/carboeur/*). If we are to more accurately assess the contributions of terrestrial ecosystems to the global carbon budget, we must take into consideration the entire landscape mosaic, which consists of an arrangement of different, interacting ecosystems. However, very few data are available for disturbed ecosystems to serve as baselines for scaling-up efforts. Thus, there is a critical need for predicting net carbon exchange (NCE) under different disturbance regimes and at different stages of development (Wofsy and Hollinger 1997, Clark and others 1999, Schimel and others 2000).

The objective of this paper is to present a working framework for studies of carbon sequestration across complex land mosaics under intensive influences of natural and human disturbances based on our ongoing study in northern Wisconsin, USA. Within this framework, our goal is to present a suite of testable working hypotheses, justifications, empirical data, and potential scientific methods to examine and predict the cumulative carbon sequestration of complex land mosaics under different climate and disturbance scenarios.

We propose a framework for future studies of broad-scale carbon flux based on the central idea that the cumulative NCE of a landscape is determined by the land mosaic. The ecosystems within a land mosaic differ in their NCE because of variations in species composition, age structure, stand structure, ecosystem processes, microclimate, and biophysical controls on carbon flux. Therefore, a multiscale approach is needed to address the problem, as finer-scale factors influence broad-scale calculation of NCE.

Our general approach combines empirical data with existing models and remotely sensed imagery at different hierarchical levels to quantify carbon exchange at the landscape level (Figure 1). Direct measurements of carbon exchange (e.g., NCE, respiration, and photosynthesis) can be combined with biometric calculations of annual production and models of ecosystem processes (e.g., PnET); (Aber and others 1995) to provide ecosystem-level estimations of NCE and associated measurements for belowground and aboveground production. These data can then be incorporated into a land mosaic based on the structure of the landscape as determined by remotely sensed images. Further, predictions of landscape-level NCE under different land-use or disturbance scenarios can be obtained by linking spatial models, such as HARVEST (Gustafson and Crow 1994), to ecosystem-level NCE.

Landscape Structure

The idea that landscape structure is crucial for quantifying landscape-level NCE is central to our framework. Landscape structure has been described traditionally using a patch–corridor–matrix model (Figure 2a), in which land mosaics are described using only these three structural features (Forman 1995). However, research has suggested that landscape structure is not just a simple spatial configuration of multiple ecosystems, but rather a complex mosaic that includes transitional zones—areas of ecosystems that are influenced by structural edges (i.e., area-of-edge-influence; AEI), such as between two or more ecosystems or adjacent to linear features such as roads (Chen and others 1992, 1996, Angold 1997, Forman and Deblinger 2000, Watkins and others 2003). In many fragmented landscapes, the AEI, which depends on surrounding landscape structure, has different composition, structure, soils, and microclimate than interior forests (Chen and others 1995, Matlack 1993, 1994). Past research has emphasized the unique influences of forest edges on various ecological properties, including microclimate (Matlack 1993, Chen and others 1995, 1999), animal behavior and diversity (Gates and Gysel 1978, Yahner 1988, Didham 1997), and plant distribution and diversity (Matlack 1994, Euskirchen and others 2001, Harper and Macdonald 2002). It has also been shown that growth rates of vegetation decrease and mortality increases near the edge (Chen and others 1992), potentially because of increased exposure to sunlight and wind, as well as amplified competition. Therefore, the NCE of the AEI will be different from the interior area because of different biophysical and physiological controls of carbon flows. Laurance and others (1997) argued that productivity of tropical forests declined by about 36% as a result of edge creation. At our study site

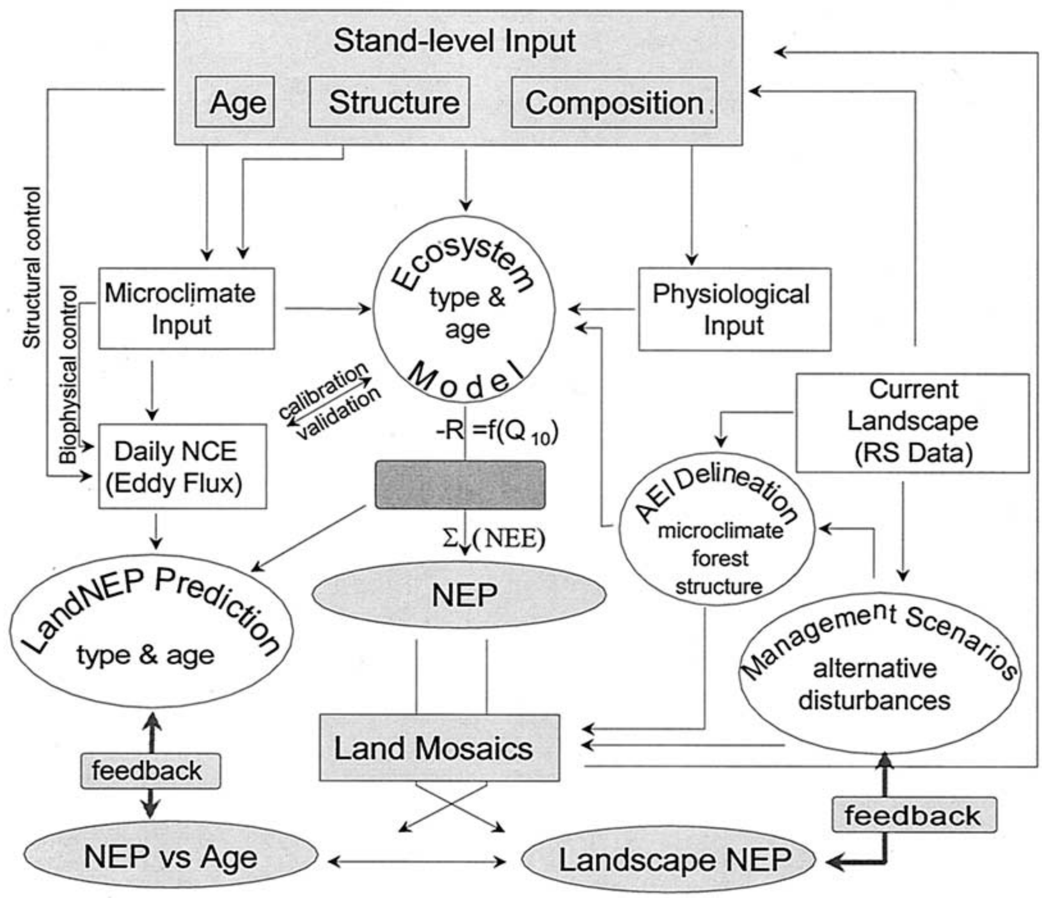

Figure 1. Conceptual framework for studying landscape-level carbon flux and storage in disturbed land mosaics, with explicit consideration of disturbance regime and landscape structure, including the area-of-edge influences (AEI).

in the Chequamegon National Forest in northern Wisconsin, Brosofske (1999) found that 20%–25% of the landscape falls within 50 m of edges. Clearly, we cannot ignore the AEI if we are to more accurately assess broad-scale net ecosystem production (NEP).

Enough is currently known about single-edge influences that attempts at constructing a generalized theory of edge influence are underway. However, these prior studies are limited by their restricted focus on high-contrast forest–clear-cut or forest–agricultural edges, and they do not consider areas that are influenced by multiple AEI or lower-contrast edges. Yet, it is reasonable to assume that the effects of these other types of edges may be different. For example, one would expect that lower-contrast transitional zones, such as between two different forest types, might have influences of lesser magnitude than do high-contrast edges, whereas areas influenced by multiple edges may have greater or qualitatively different effects on ecological properties and processes. In many disturbed land mosaics, areas that are influenced by multiple features predominate when viewed from a landscape perspective (Franklin 1993, Chen and others 1996, Zheng and Chen 2000). Clearly, AEI needs to be incorporated into the landscape mosaic (Figure 2), with attention to the specific characteristics of the single or multiple edges influencing the area. In this paper, we suggest that treating AEI as a separate landscape element in ecological studies will provide more accurate information concerning the land mosaic, particularly in disturbed landscapes.

Hypotheses and Justifications

Generating testable hypotheses at broader spatial scales (e.g., landscape and regional levels) is extremely challenging. Using the overriding concept that the cumulative NCE of a landscape is determined by the land mosaic, or the types and arrangements of ecosystems present, we present four working hypotheses for consideration and potential adoption in studies of carbon sequestration.

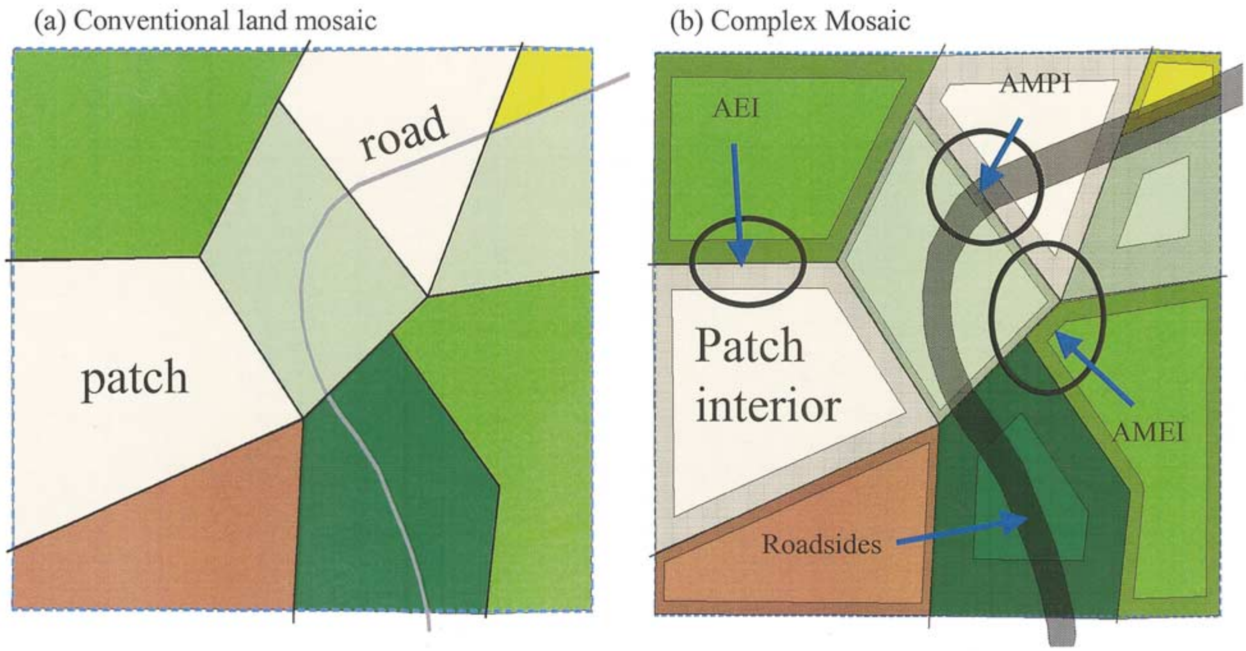

Figure 2. Schematic illustration showing (a) the conventional depiction of landscape structure consisting of patches and corridors within the matrix, and (b) a more complex depiction of the land mosaic, within which transitional zones (e.g., areas-of-edge-influence, AEI, adjacent to both corridors and patches; areas-of-multiple-edge-influences, AMEI; and areas-of-multiple-patch- influences, AMPI) have been delineated and are treated as distinct landscape elements within the land mosaic.

Hypothesis 1: The area of an ecosystem that is influenced by structural edges (area-of-edge-influence, AEI) has NEP that is significantly different from the ecosystem interior. Thus, landscape-level NEP is not simply the sum of the NEPs of the individual ecosystems present multiplied by their areas; it is also dependent on interactions between the ecosystems (Figure 2).

Numerous studies have shown clear differences in microclimatic and vegetation characteristics near edges (Chen and others 1992, 1995, Brosofske and others 1999, Matlack 1993, 1994). Since these variables directly control NCE (Aber and Federer 1992) and are necessary parameters for the most applicable ecosystem process models, we expect that the AEIs will have different NCE predictions than the NCE of the ecosystem interior and of other AEIs. Because (1) disturbed landscapes often contain a large amount of AEI, (2) the amount of edge is related to the arrangement of ecosystems relative to one another, and (3) different disturbance scenarios are likely to result in dissimilar landscape mosaics, cumulative NCE will differ for most disturbed landscapes even if they are similar compositionally. In examining the amount of CO_2 released from soils near forest edges, Oberbauer and others (1996) found that soil carbon efflux within 25 m from the edge is twice that in the forest interior. If a significant portion of the landscape is classified as AEI, calculations of cumulative respiration over the landscape should account for AEIs. Although the size of individual AEIs prohibits direct measurement of NCE using eddy-covariance systems, NCE can be estimated using ecosystem process models with empirical structural and microclimatic data while assuming constant photosynthetic responses by species.

Hypothesis 2: Age structure and composition of an ecosystem play critical roles in determining the ecosystem's contribution to cumulative NEP of the landscape mosaic.

Following a disturbance, the NCE is regulated largely by the decay of roots, woody debris, and litter, while carbon uptake by green plants is low because of the low leaf area; this results in a net carbon release to the atmosphere by regenerating stands (t_1, Figure 3A). As aging and succession proceed, NEP increases (t_2), peaks (t_3), and returns to a relatively stable stage (t_4, Figure 3A) (Harmon and others 1990, Arneth and others 1999, Schulze and others 2000). However, relative rates of photosynthesis and respiration vary with age, structure, and species composition (Clark and others 1999, Law and others 2001, Chen and others 2002). For example, a few studies have suggested that old forests may still be carbon sinks. The amount of carbon

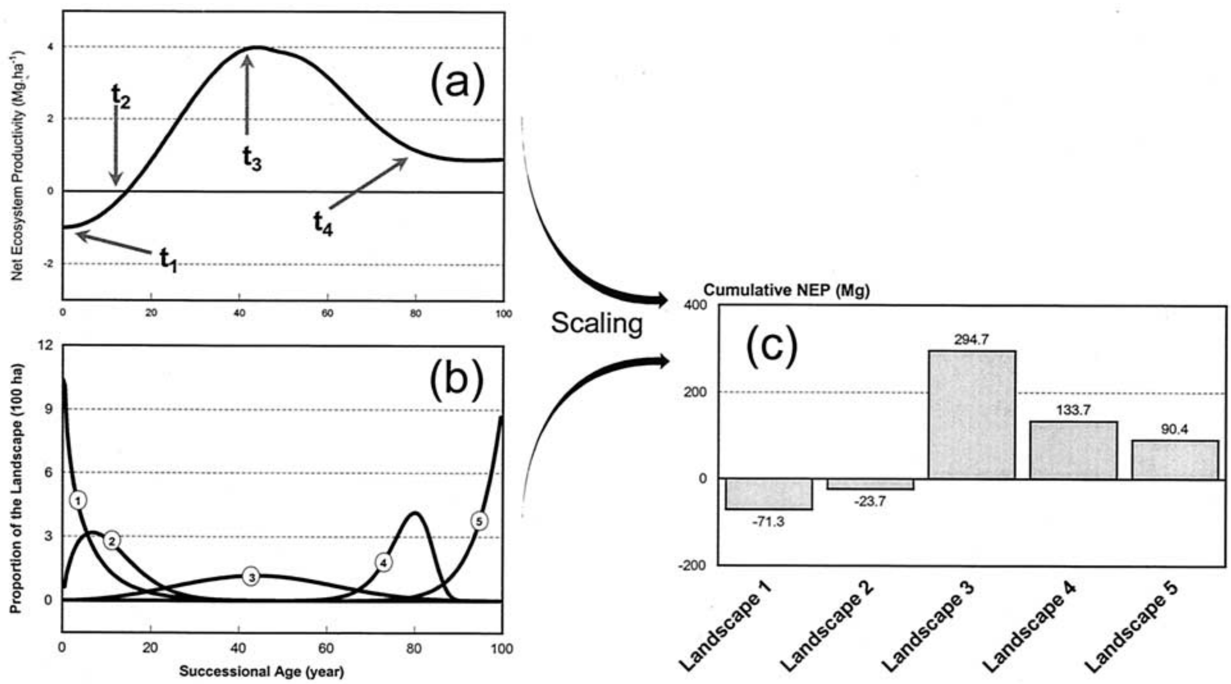

Figure 3. Hypothesized changes in net ecosystem production (NEP) with developmental age in a particular ecosystem (a) acts in concert with the age structure of the landscape (b) to determine the cumulative NEP of the landscape (c). In (a), t_1–t_4 identify four different time periods along the developmental spectrum for comparison. In (b), the age structures of five hypothetical landscapes are given, with the expected relative NEP for each corresponding hypothetical landscape given in (c). A 100-ha landscape can act as a carbon source when young stands (0–20 years old) dominate the landscape, or as a significant sink when mature stands are the primary components. The cumulative NEP is expected to assume an intermediate when later successional stands dominate the landscape, even though landscape biomass may be highest.

sequestered by these old forests could account for a large proportion of the missing carbon at the global scale (Carey and others 2001) (Figure 4). Thus, different ecosystem types and those in different successional stages have different ecosystem-level carbon exchanges. The relative amount of one ecosystem type versus another, or younger versus older stands, in a landscape may greatly influence its cumulative production (Figure 3C).

Hypothesis 3. The relative importance of different structural and biophysical controls of carbon exchange is ecosystem dependent.

NCE depends on the combination of a suite of environmental and physiological parameters. Although several simple models have been proposed (e.g., Collatz and others 1991, Hollinger and others 1994, Aber and others 1996, Waring and others 1995, Goulden and others 1996), ecologists are for the most part convinced that variable interactions cannot be ignored; that is, a statistical relationship based on a limited number of variables may not be applicable when values of other variables change. For example, soil respiration is generally believed to increase exponentially with temperature (i.e., Q_{10} model), but this relationship also depends on soil moisture, litter quality and quantity, and vigor of vegetation growth (O'Connell 1990, Raich and Schlesinger 1992, Davidson and others 1998). These combinations of variables will differ by ecosystem, and thus the relative importance of each variable will be ecosystem-dependent.

Within the Chequamegon National Forest in northern Wisconsin, soil respiration rates were found to be highest in regenerating hardwood stands and lowest in clear-cuts and pine barrens; the Q_{10} response varied as much among the ecosystems within the landscape as it does on a regional or global scale (Euskirchen and others 2003). In addition, although soil temperature was an accurate predictor of soil respiration within the ecosystems on a weekly basis, among ecosystems litter depth (as an indicator of aboveground net primary productivity) was a better predictor of seasonally averaged soil respiration (Figure 5) (Euskirchen and others 2003).

Hypothesis 4: The frequency and intensity of disturbances in time and space control the cumulative NEP of the land mosaic through alteration of ecosystems

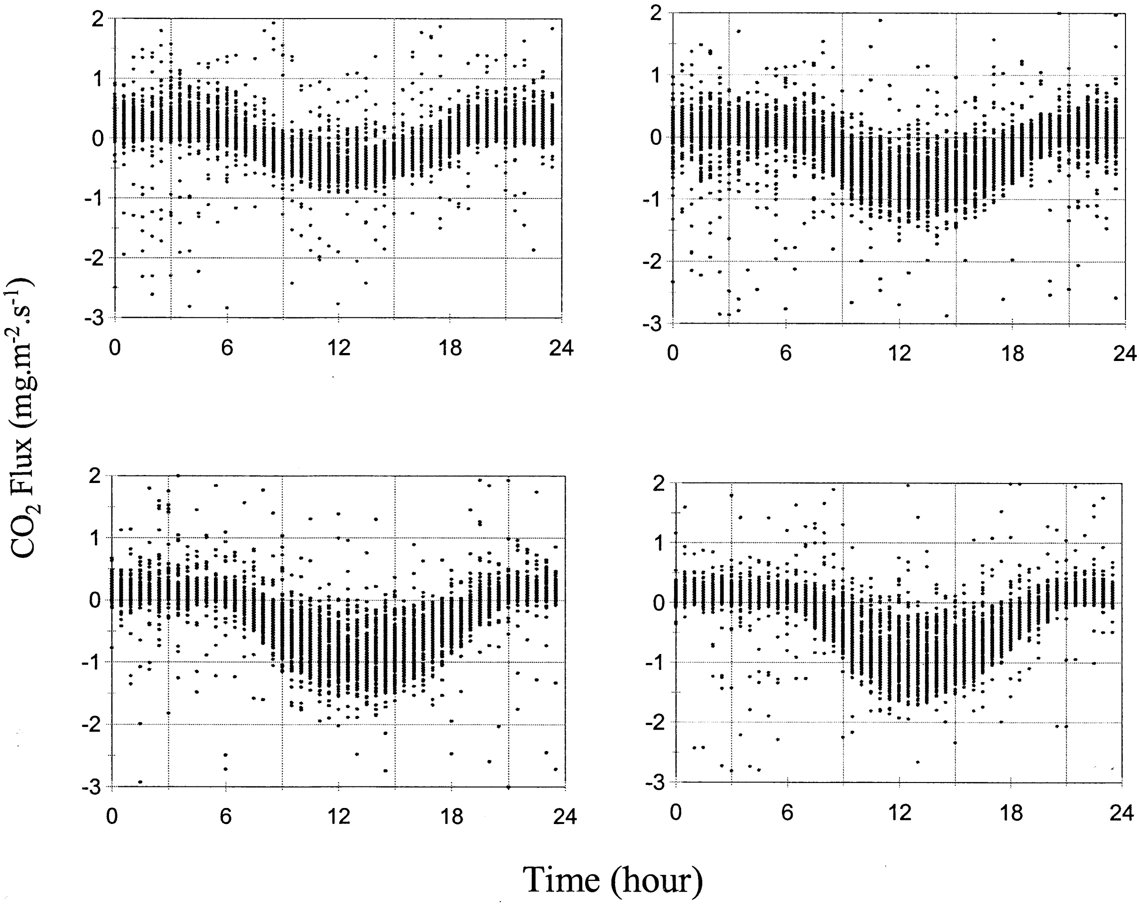

Figure 4. Diurnal patterns of net exchange of CO_2 (30-min means) in young and mature hardwood and conifer forests (i.e., two dominant ecosystem types) in the Chequamegon National Forest, Wisconsin, USA Data were calculated based on eddy-covariance measurements at four canopy-access towers. Negative values indicate carbon assimilation (i.e., net carbon gain) and positive values indicate net carbon loss.

that vary in age, structure, physical environment, and interactions.

Disturbances that happen frequently reduce ecosystem age and inhibit successional change (Dale and others 2001). Extensive or intense disturbances alter the interactions among ecosystems by creating additional, fewer, or more extreme edge influences. Thus, based on hypotheses 1 and 2, cumulative NCE will reflect these changes. Moreover, the NCE for a given ecosystem type in the scenario depicted in Figure 3 could vary greatly depending on the age of the ecosystem. For example, Euskirchen and others (2002) developed a model, LandNEP, to assess how alternative management strategies applied to hypothetical landscapes can result in varying levels of carbon sequestration. In the model, each ecosystem within the landscape was assigned to a disturbance interval (e.g., a rotation age for timber harvest) and to a Weibull-exponential distri-

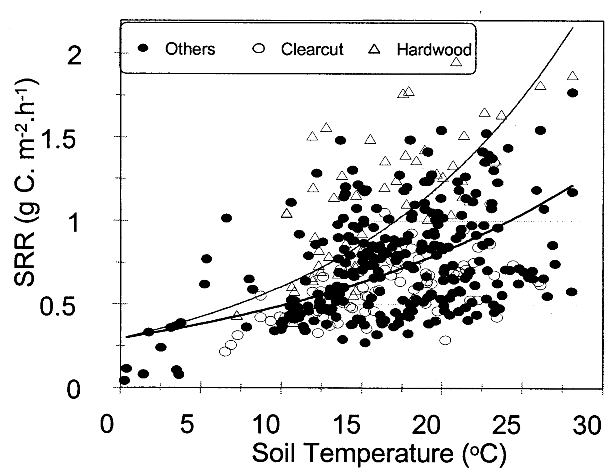

Figure 5. Relationship between soil respiration rate and soil temperature within six patch types in the Chequamegon National Forest, Wisconsin, USA.

bution (Carey and others 2001). A set of parameters was used to determine *NEP* for a particular simulation year. In one of the predictions, the authors found that the maximum *NEP* for an ecosystem aged 44 years was 1.5 Mg C/ha, but the *NEP* at the disturbance interval of 25 years was only 0.4 Mg C/ha. The ecosystem with more frequent disturbances never reached its maximum potential as a carbon sink, which is generally the case in naturally occurring and managed stands (Euskirchen and others 2002). Furthermore, a sensitivity analysis demonstrated that an increase in the disturbance interval could alter an ecosystem's role from a net carbon source to a carbon sink. Although this model is hypothetical, it provides a good indication that disturbance frequency and intensity will influence the structural and physical characteristics of the landscape mosaic and thereby alter *NEP* at the landscape scale.

The effect of management practices may vary depending on the ecosystem type to which they are applied. For example, a clear-cut in a hardwood stand often results in a substantial amount of woody debris being left behind, whereas in pine stands a greater proportion of aboveground biomass is harvested for economic reasons. This results in a lower amount of debris and therefore lower respiratory carbon loss during the early years of regrowth in pine than in hardwood stands, allowing the former to reach a positive carbon balance sooner. The uncertainties of carbon flux estimations that are unavoidable as a result of the disturbance/harvesting initially depend on the degree of environmental disturbance and will decrease with increasing interval between the disturbances.

Research Approaches

Because of scaling issues and the complexities involved in determining carbon flux across multiple ecosystems within a landscape, developing a sound design for broad-scale studies to test the hypotheses presented necessitates using a combination of several conventional methods. While it is difficult to develop a landscape-level experiment to test these hypotheses directly, one can collect or generate data in disturbed land mosaics to model changes in the cumulative carbon flux across the landscape. We describe below five methods commonly applied in ecosystem studies (see also Table 1). For studies of carbon flux at broad scales, data based on more than one method are necessary as they reveal different aspects of carbon cycling.

Biometric Estimations

This method involves field measurement of carbon pools and annual increments, such as aboveground (i.e., sum of stems, branches, leaves, etc.) and belowground biomass (sum of fine and coarse roots, litter layer, organic carbon, soil fauna, etc.) in repeated plots for a target ecosystem (Clark and others 2001). Data sets are often widely available from current and historical forest inventory efforts (e.g., Forest Inventory Analysis, FIA) (Birdsey 1992, Turner and others 1995) and can be used to evaluate carbon sequestration. This technique has evolved from community and ecosystem ecology and requires little instrumentation and maintenance but long-term commitment from the research team. Results based on this approach are considered more reliable by ecologists on an annual basis and, hence, can be used for cross-examination of carbon fluxes measured using other methods (Curtis and others 2002). However, accurate sampling of belowground components and changes at finer temporal scales (<1 year) is extremely difficult, and even impractical when multiple ecosystems are involved (Clark and others 2001).

Ecosystem Modeling

Perhaps the only method available for testing all the hypotheses, including predictions of carbon flux under a variety of environmental and disturbance scenarios, this approach requires empirical data for model parameterization and validation (Aber and others 2001). Often, required input data are unavailable or expensive to collect; indeed, data may be impossible to collect under certain circumstances, such as at broader spatial and temporal scales. An alternative is to apply actual data in model parameterization and examination to increase the confidence level for model predictions. Once the models have been developed, however, this approach can provide useful predictions and the ability to simulate complex ecosystems and test the outcomes of alternative land-use change or disturbance scenarios.

Applications of Remote Sensing and Geographic Information Systems (GIS)

Remote sensing techniques provide promising means for carbon studies, especially for broad spatial scales (Brown and others 1993, Iverson and others 1993, Bergen and Dobson 1999). Remotely sensed imagery can be obtained quickly and easily for the entire study area, from watershed to global scales, and for the same areas at high revisit frequencies. Such advantages allow scientists to examine global net primary production (NPP) and its interannual variability (Prince and Goward 1995, Goetz and others 2000, Running and others 2000), one of the necessary aspects of studying the global carbon balance and climate change. The underlying justification for application of remote sens-

Table 1. Comparisons of five conventional methods for examining terrestrial ecosystem carbon flux and storage

Methods	Advantages	Disadvantages
Biometric	Simple concepts and methods	Point measurements of a landscape
	Little technology or equipment required	Inadequate estimates of belowground biomass
	Widely used since IBP (International Biosphere Program)	Lack of fine temporal resolutions
	Current and historical inventory databases widely available (e.g., FIA—Forest Inventory Analysis)	Long-term commitment
	Good estimates of aboveground biomass	
	Structurally based	
Ecophysiological	Process based	Scaling up to broader scales difficult
	Controlled experiments possible	Sophisticated instrumentation required
	Fine temporal resolution	Does not provide estimates at ecosystem level
	Focus on specific processes	Expensive
	Provides necessary parameters for modeling	
Micrometeorological	Direct measures of carbon flux	Specific site, large fetch requirements
	Automatic, continuous measurements	Limited number of adequate sampling locations
	Easy to replicate	Sophisticated instrumentation
	Less potential for human errors	Difficult to maintain
	Process-based	Special knowledge required
		Very expensive
Remote sensing/ geographic information systems	Large area encompassed (i.e., landscape estimates possible)	Discontinuity at fine temporal scales
	Frequent revalidation feasible	Meticulous corrections needed
	Diverse historical and current databases available	Limited spatial and spectral resolutions
	Quick data acquisition (e.g., real-time)	Two-dimensional view of a three-dimensional space
	Potential linkage to ecosystem properties	Indirect measurements
Modeling	Prediction and scenario testing	Extensive information needed for model parameterization and validation
	Simulation of complex ecosystems	Limited applicability among ecosystems
	Inexpensive and efficient	Outputs can vary significantly among models
	Multiple scale applications	

ing to the estimation of terrestrial NPP is based on two facts: (1) NPP is directly related to the amount of solar energy that plants absorb (absorbed photosynthetically active radiation, APAR) (Monteith 1972, 1977); and (2) APAR can be estimated from remotely sensed imagery (Sellers 1987, Asrar and others 1992, Myneni and others 1997). Among the several forms of spectral vegetation indices derived from remote sensing data, the normalized difference vegetation index (NDVI) is the most widely used as an analog of leaf area index (LAI), which is related directly to APAR. Consequently, NDVI can reflect not only the carbon dynamics within the current landscape, but also spatial changes in the landscape mosaic over time for broad areas of interest. Some of the disadvantages of this indirect approach include its inability to examine fine temporal scales within ecosystems, as well as its limitations in spatial and spectral resolutions.

Micrometeorological Methods

An increasing trend in carbon studies involves application of micrometeorological methods such as eddy-covariance (see Figure 4), mass-balance, Bowen ratio, and surface renewal analysis in direct measurement of carbon flux (Rossi and others 2002, Paw U and others 1995). These methods, widely used in several major initiatives (e.g., AmeriFlux Network, http://public.ornl.gov/ameriflux/), involve installation of access towers above the canopies and require sophisticated equipment and unique expertise in atmospheric physics, with the result that only a limited number of sites can be studied. A major limitation of these micrometeorological techniques is their requirement for large fetch and relatively flat sites, which limits their applicability for studies of area-of-edge-influence. Installation of sensors on aircraft can cover multiple ecosystems, providing an overall estimate for the landscape or region (e.g., Crawford and others 1996), but it can less easily partition out the contributions of particular ecosystems. In addition, aircraft measurements are feasible only for a limited time, thus providing snapshots in time that limit their usefulness for temporal studies. An alternative is to develop a suite of mobile eddy-covariance towers so that multiple ecosystems can be studied at the same time (Eugster and others 1997, Chen and others 2002). Mobile towers, although prohibitively expensive, can provide direct, continuous records of net ecosystem exchange of carbon from very fine temporal scales (e.g., minutes) to long-term (i.e., multiple years) dynamics. Special attention to flux corrections caused by low horizontal wind speed, nighttime dynamics, and advectional effects is needed for high quality results (Paw U and others 2000, Massman and Lee 2002).

Ecophysiological Approach

The response of individual plants or metabolic processes to specific environmental parameters has been studied in great detail, and the knowledge gained forms the basis for studies of higher order systems. For example, the universal quadratic relationship between light intensity and CO_2 exchange is being used from the individual chloroplast level to the ecosystem level. The plant growth and ecosystem exchange models that utilize mechanistic understanding of particular processes are generally preferred over those that are based on empirical relationships. Physiological processes must remain coupled and in balance with one another, and this provides an opportunity to cross-check the accuracy of different measurements and modeled predictions. For example, the fact that the exchange of water vapor and CO_2 are correlated has been used to predict branch level photosynthesis from the measurements of branch sap flow (Morén and others 2001). Although ecosystem level measurements of carbon and water vapor exchanges can be validated against plant-level measurements of net photosynthesis and transpiration, as well as with that of stem sap flow, one must be careful when extrapolating from one scale to another. While some parameters can be used readily across scales, others do not translate clearly. For example, in scaling transpiration from leaf to canopy and landscape level, one must abandon stomatal conductance and instead consider the roles of boundary layer conductance and advection that become important considerations on scales higher than leaf-level (Waring 1993). At the other end of the spectrum, one could consider soil respiration rate (SRR), which is empirically calculated using soil temperatures, soil moisture and soil aeration (Figure 5). Frequently, relationships with temperature provide very high predictive power and the relationship can be used from single root to ecosystem scale. However, the universalities are rare and could be modified by other, more limiting factors. In the case of SRR, low soil moisture may invert the usually positive relationship (Ma and others, this issue).

Clearly, no single method can be employed to accurately quantify cumulative carbon flux across a land mosaic. Ecosystem delineation and stand characteristics are best determined at the landscape-level using remote sensing techniques. Because of the practical impossibility of obtaining enough direct flux measurements for all ecosystems over time, information about simultaneous carbon fluxes of all the ecosystems must rely on ecosystem models that have been properly parameterized using ecophysiological and biometric data and validated using direct measurements of NCE from micrometeorological methods. The ecophysiological approach can provide us with additional information concerning the potential mechanisms controlling carbon flows within the ecosystem, but scaling the processes from individuals to ecosystem or landscape scales is challenging (Vourlitis and others 2000). Direct measurements of NCE provided by the eddy-covariance method can be used for necessary justifications of respiration models (e.g., Q_{10}) and ecosystem models (e.g., PnET). If accurate, the approach could be applied more generally, reducing the need for expensive, time-consuming, direct measurements of carbon exchange. In conclusion, the framework proposed in Figure 1, including associated measurements, is suggested as a sound foundation for addressing the proposed hypotheses and meeting the objectives of broad-scale carbon studies.

Conclusions

Accurate quantification of carbon exchange at the landscape level, particularly with regard to disturbed landscapes containing different successional stages and explicit recognition of the role of the area-of-edge-influences in the overall mosaic, clearly represents a knowledge gap in the current scientific arena. In addition to increasing our understanding of the feedbacks between various land mosaics and cumulative *NEP*, our ongoing efforts and those of the CarboEurope

Cluster will constitute the first initiatives linking the fragmentation process and ecosystem productivity by explicitly addressing contributions of AEI and age structure to landscape-level *NEP*. Results based on our framework could greatly advance current landscape management efforts in many regions of the world where forests are being rapidly fragmented into smaller, isolated patches. In this pioneering work, linkages will be made between ecosystem- and landscape-level carbon exchange to determine the relative influences of each ecosystem to cumulative *NEP* using process models at different hierarchical levels within a GIS framework. Other than model predictions, current information about carbon exchange at the landscape level is limited, coming from either tall towers (Bakwin and others 1998) or one-time flux measurements from aircraft (Crawford and others 1996); neither method can partition the ecosystem-level contributions to landscape carbon exchange. By investigating how forest disturbance processes, individual disturbed and intact ecosystems, and ecosystem interactions influence broad-scale carbon exchange, we can gain a more accurate understanding of how such disturbance scenarios might influence the role of terrestrial ecosystems in the context of the global carbon budget (Prentice and others 2000).

Acknowledgements

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